PRESIDENTIAL ADDRESS

EVOLUTION AND CLASSIFICATION IN *EUCALYPTUS*

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Synopsis

Following general discussion of some principles of classification, some probable evolutionary trends in *Eucalyptus* are discussed, especially in relation to the recent classification of Pryor and Johnson (1971). Particular stress is laid on the multiple trends and varied final conditions in the calyx and corolla, which are more or less opercular, and in the inflorescence. Characters of anthers, ovules and seeds, cotyledons, hairs, oil glands and ducts, and associated insects are also reviewed as expressed in the eight subgenera recognized (including *Angophora*). Suggestions are made as to the phylogenetic connections of some subgenera and sections, and some problems of relationship are indicated within the eucalypts and between them and other Myrtaceae, which may respond to further detailed investigation and critical synthetic and analytical evaluation. A few changes in the Pryor and Johnson scheme are made or suggested.

" Our reasonings grasp at straws for premises and float on
gossamers for deductions."
　　　　A. N. WHITEHEAD, *Adventures of Ideas* (1933).

ON CLASSIFICATION

Four years ago (Johnson, 1968) I expatiated from this chair on the philosophy, methodology, problems, and especially the limitations of taxonomy in general. I concluded that no optimal classification was definable, much less attainable, whether on a phenetic or a phyletic basis, but that " none the less, the elucidation of phylogeny can still proceed, and our unperfectable classifications can still be improved by reducing inconsistency until uncertainty or instability renders further change unprofitable ". No group of Australian plants has had so many investigators as the so-called genus *Eucalyptus*, yet such is its complexity and so many the gaps in our knowledge that its classification is still manifestly improvable, and its detailed phylogeny still not elucidated.

Recently my colleague Lindsay Pryor and I have published, in skeletal form, a new scheme of classification of the eucalypts (Pryor and Johnson, 1971). In deriving this scheme and in our own current revision of it, we have had to consider characters from as many fields as possible, and to evaluate them as to evolutionary significance. As I hope to have shown in 1968, a truly theory-free classification of organisms is an impossibility, although one may certainly develop classifications for which there is no defined theoretical foundation and in which the underlying theoretical assumptions are confused and frequently unconscious.

If the distortions due to these assumptions are so multifarious and chaotic as to be evenly spread, constituting " white noise ", and if this background " noise " is not too great, some meaningful set of signals may be extracted from a phenetic analysis based on many characters. It is then up to us to interpret, in some scientifically or pragmatically profitable way, the results of the analysis. For this purpose, the " results " should not be taken as merely one particular hierarchical classification as represented by the dendrogram produced by a particular strategy. Whenever we proceed from the data to a dendrogram we lose information, and many topologically as well as metrically different dendrograms (and thus formal classifications) can be produced from a given set of data, merely by quite defensible manipulation of the strategies employed, as Lance and Williams (1967 ; Williams, unpub. 1971) have very clearly shown.

If, then, we wish to make effective use of phenetic analysis to generate hypotheses (i.e. for " interpretation " of taxonomic data) we shall need to consider *various* dendrograms and also to check back frequently to the characters themselves. Such hypotheses may relate to the prediction of properties (including genetic and physiological behaviour) of taxa and individuals. A " general " classification is supposed to be widely useful for such prediction, and we may claim that the Pryor and Johnson system of 1971 (which I shall designate PJ_1 for convenience hereafter) meets this criterion better than any other yet available for *Eucalyptus*, although it is bound to be seriously in error at certain points, some of which are already apparent (see below). Predictivity may be improved in this case also by going beyond the generalized summary given by the classification to the particular data from the individual taxa concerned. I should say here that PJ_1 is not based on a numerical analysis, is explicitly not a neo-Adansonian system which claims to give characters " equal weight " (a will-o'-the-wisp notion at best), and is not theory-free. Nevertheless, it is phenetically based to a considerable degree, and the foregoing remarks on broadly-based phenetic classifications are applicable to taxonomic work of this kind and not only to taximetric studies.

Another kind of hypothesis is the phylogenetic, which may be said to imply retrospective prediction ; that is, it predicts what we may hope to find out, in the future, about the past—and thus " explain " the present ! Since we accept, as indeed most pure pheneticists do, that the characters of organisms which are important to them, and to us, are determined largely by their evolutionary history, we inevitably become involved in partial circularity of argument if we base our classifications themselves to some degree on phylogenetic considerations and interpretations. The building of such partially phylogenetic classifications involves some positive feedback from conclusions to argument, and hence incurs stern disapproval from those who seem to think that scientific investigation and interpretation should depend on simple elementary logic. This is an over-simplification and the use of phyletic reasoning in classification, provided that it is subjected to checks and balances, has been defended by various authors (for discussion and further references see Johnson, 1968, 1970 ; Hull, 1967 ; Ghiselin, 1969).

It is also possible to develop more or less defensible models for the derivation by numerical methods of cladistic reconstructions, which may or may not then be used for classification.

We have not used taximetrics of either kind in *Eucalyptus*, because the detailed accumulation of numerical data, species by species, has not been possible on a sufficiently reliable basis. Recent studies by ourselves and others, notably D. J. and S. G. M. Carr (for references see Pryor and Johnson, 1971), all serve to show how much morphological misinterpretation (that is, false homology) there has been in eucalypt descriptions up to the present. I would hope that within the next decade it will indeed be feasible to carry out taximetric analysis both by variable-strategy phenetic techniques and by the use of phyletic (cladistic and perhaps patristic) models, and that these studies will employ accurately expressed and interpreted data. Such work may enable us (i) to add to the general usefulness of our classification which will, however, always remain a compromise, (ii) to compare the character associations themselves more effectively in relation, say, to their adaptive significance, and (iii) to reconstruct more plausibly the phylogenetic history.

In the meantime we have PJ_1, already developing towards PJ_2.* What does it summarize for us in the evolutionary history of the eucalypts and what questions for future investigation does it help to define ? (We shall not here discuss its practical usefulness, important as that is.)

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* A step in this development is the publication of new taxa and formalization of changes of status foreshadowed in PJ_1, by Johnson and Blaxell (in press, *a* and *b*).

The Classification Adopted

PJ$_1$ recognizes eight main groups within the eucalypts, which are displayed in Figs 1, 4 and 5 and Table 1. We have arrived at these by agglomeration of similar species and division according to apparent major gaps in the continuity of character variation. They correspond in general to fertility groups. No case is known of successful interbreeding, even to F$_1$ stage, between any of these groups, although interbreeding is common within groups, and particularly within sections. Fertile intersectional hybrids are also known in a number of cases, but none involve the sections EA, EF, SB, SS, SD or SW. (Hereafter I shall use the code designations of sections and lower taxa, an integral part of PJ$_1$. The coding for each subgenus is the same as the initial letter of its name.)

Table 1

Distributional Synopsis of Eucalyptus *Classification* (PJ$_1$)

Regions: Q=Queensland, N=New South Wales, V=Victoria, T=Tasmania, S=South Australia, W=southern half of Western Australia, south of 26° S, K=northern half of Western Australia, Y=Northern Territory, M=Malesia (incl. New Guinea). Modal or near-modal values are italicized. For " No. of subseries " a non-subdivided series is counted as one subseries. The columns are additive, the rows are not so because of overlapping distributions (e.g. W and K together total 191 species). Taking superspecies and subspecies levels respectively (rather than species) as units, the totals for the genus would be 316 (superspp.) and 531 (subspp.).

SUBGENUS Section	No. of Series	(No. of Subser.)	Code	Q	N	V	T	S	W	K	Y	M	Total Species
ANGOPHORA ..			A										[7]
Liberia	1	(4)	AA	5	7	1	—	—	—	—	—	—	7
BLAKELLA ..			B										[9]
Lemuria	1	(1)	BA	6	1	—	—	—	—	6	6	2	9
CORYMBIA ..			C										[33]
Rufaria ..	4	(6)	CA	11	5	1	—	2	5	*15*	*14*	2	25
Ochraria ..	3	(3)	CC	7	3	1	—	—	—	—	—	—	8
EUDESMIA			E										[15]
Quadraria ..	2	(5)	EA	2	—	—	—	2	*9*	4	4	—	10
Apicaria ..	2	(3)	EF	*4*	1	—	—	—	—	3	2	—	5
GAUBAEA			G										[2]
Curtisaria ..	1	(1)	GA	2	—	—	—	—	—	—	—	—	2
IDIOGENES.. ..			I										[1]
Gympiaria ..	1	(1)	IA	*1*	—	—	—	—	—	—	—	—	1
MONOCALYPTUS (=EUCALYPTUS *s. str.*)			M										[91]
Renantheria ..	9	(26)	MA	15	*64*	23	11	7	14	—	—	—	91
SYMPHOMYRTUS			S										[285]
Equatoria ..	2	(2)	SB	*2*	—	—	—	—	—	1	1	1	4
(incl. *Howittaria*)			(SS)										
Tingleria ..	1	(1)	SD	—	—	—	—	—	*1*	—	—	—	1
Transversaria ..	2	(5)	SE	10	11	2	—	1	1	—	—	—	14
Bisectaria ..	18	(23)	SI	4	8	5	—	16	*85*	8?	7	—	93
Dumaria ..	4	(6)	SL	—	2	2	—	8	*28*	1	—	—	31
Exsertaria ..	3	(8)	SN	*17*	15	5	—	2	2	11	8	3	30
(incl. *Umbra-warria*)			(SQ)										
Maidenaria ..	2	(11)	SP	9	*35*	24	13	3	—	—	—	—	46
Adnataria ..	11	(17)	SU	*40*	33	16	—	13	4	9	10	—	65
Sebaria	1	(1)	SW	*1*	*1*	—	—	—	—	—	—	—	1
Total species ..	..	..	..	136	*186*	80	24	54	149	58	52	8	443

It will be seen that we have included *Angophora* among the eight major groups which we have ranked as subgenera. *Angophora* has traditionally been kept apart generically from *Eucalyptus*. We are not at this stage reducing *Angophora* formally to subgeneric rank, with the consequent new nomenclatural combinations necessary under the International Code of Botanical Nomenclature, but I am myself refraining from this solely to avoid possible reverse changes if all or most of the subgenera are later accorded full generic rank. There are likely to be quite good reasons for the latter step, but certainly not for the over-simplified
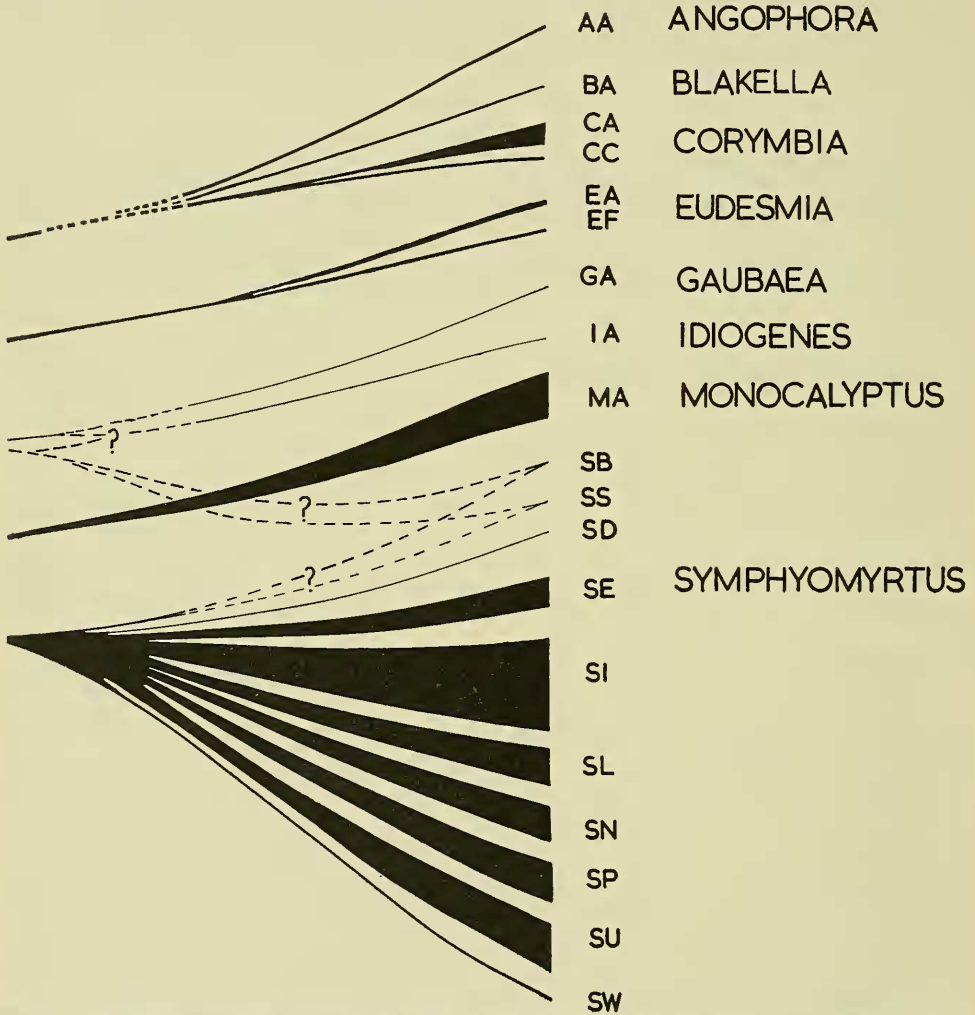
Fig. 1. Suggested general phylogeny of eucalypt subgenera and sections. Widths of branch-ends are in order of, but not proportional to, number of species. Sections designated by their two-letter codes of PJ$_1$ scheme.

two-genus proposal of the Carrs, in which "*Eucalyptus*" (*sensu* Carr et Carr) would comprise *Eudesmia, Gaubaea, Idiogenes* and *Monocalyptus* of PJ$_1$, while our remaining subgenera (except *Angophora*) would constitute "*Symphyomyrtus*" (*sensu* Carr et Carr). An inspection of Figs 4 and 5 and our suggested groupings in Fig. 1 will make clear the basis for rejecting this (see also Pryor and Johnson, 1971, pp. 16–19).

Division of *Eucalyptus* would certainly cause considerable inconvenience, even dismay, amongst those who care little about the relationships, particularly since more than half of the species (including those best known overseas) would fall into *Symphyomyrtus* (*sensu* PJ$_1$). I consider that the change should not be made until we have a rather better-developed picture of the relationships of the subtribe Eucalyptinae (*Eucalyptus* incl. *Angophora*) with the various groups hitherto referred to the heterogeneous subtribe Metrosiderinae and with other Leptospermoideae.

EVOLUTIONARY TRENDS

Eucalyptus in the traditional circumscription has been characterized chiefly by the operculate flower, and thus distinguished from *Angophora*. [The presence of floral opercula of various kinds in other clearly less closely related Myrtaceae such as *Eucalyptopsis* (perhaps somewhat related), *Acicalyptus*, *Cleistocalyx*, *Piliocalyx* and *Calyptranthes* is obviously due to convergence and is not relevant here except as indicating a certain " prospective adaptation " to this development in the family.] It is clear from comparison of inflorescences, anthers, cotyledons, oil ducts in the pith and elsewhere, leaf-venation, bristle-glands, trichomes, wood anatomy, and the occurrence of pathogens (e.g. *Ramularia*, Walker and Bertus, 1971), some of which are displayed in Fig. 4, that *Corymbia* and *Blakella* are more closely related to *Angophora* than to other subgenera of *Eucalyptus*. I think it virtually certain that these three had a common ancestral stock after their divergence from the other subgenera, as indicated in Fig. 1. Both 4-merous and 5-merous flowers occur in *Angophora* and to convert an *Angophora* into a *Corymbia* requires little more than " operculization " by concrescence of sepal and petal primordia into rings shortly after their initiation, combined with some modification of flowering and fruiting hypanthia and of trichomes. Even in *Angophora* the petals are broad-based and possess thick triangular median regions which are effectively valvate in the bud (though the thinner margins are imbricate). Formation of an operculum from such a flower-structure seems a more likely phylogenetic event than in most Myrtaceae, where the petals have a narrow basal " claw " and are thin-textured throughout. *Arillastrum*, which may be significant in this regard, will be discussed later.

Thus we are led to consider the possible or probable trends in the evolution of various organs or other attributes of eucalypts, and of their association in the several groups. I can deal with these only in summary fashion; further discussion and most relevant references will be found in Pryor and Johnson (1971), and it is assumed that the general morphology of eucalypts is familiar. The opercular structures and the inflorescence are at present perhaps best known, but have been much misunderstood until recently. The trends in these are complex and will be treated first and most fully.

(1) *Opercular Structures*. The range of these is illustrated in Figs 4 and 5. Pryor and Knox (1971) give an account of their development in various groups. One or both perianth whorls are opercular due to formation of a ring meristem, except in *Angophora* and presumably in ancestral forms. In all cases, however separate primordia are present at the initial stages and the separate tips into which these develop are often more or less discernible even in mature buds. Both calyx and corolla are normally tetramerous, each with two decussate pairs of tips, but fives are most common in *Angophora* and may be found in occasional flowers of some species of other subgenera (e.g. in *Gaubaea* and in SUNCC *E. porosa* of *Symphyomyrtus*), while in *Monocalyptus* there is only a single (calycine) whorl with usually only two initial primordia present. It is perhaps conceivable that the opercular condition of the corolla is monophyletic. However, I think this very unlikely in view of the lack of resemblance in other characters between the angophoroid group (subgenera A, B, C) and others, as well as other distinctive

features amongst some of the latter as discussed below.   The calycine operculum (where it occurs) *cannot* be monophyletic.   Opercular conditions can be classified into the following types (*italicized* letters refer in a complex but mnemonic way to operculum-types ; PJ_1 code symbols are in roman) :

Type A : *Calyx* of free persistent sepals ; *corolla* of $5 \to 4$ free broad-based petals : Generalized ancestors, also *Angophora*.

Type $E(A)G$: *Calyx* of free persistent sepals (often small due to early cessation of growth) ; *corolla* (initially 4-tipped) opercular : *Eudesmia* section EA *Quadraria* (most species, see below) : *Gaubaea*. [These derived* *independently* from *early* generalized ancestors of type A, not from *Angophora*.]

Type $E(F)$: *Calyx* of free tips in very early bud but basal meristematic rings of calyx and corolla becoming united early in development, so that the sepal tips (often becoming extremely obscure) are carried high on the operculum of *calyx and corolla* : *Eudesmia* section EF *Apicaria*, also in various intermediate conditions from Type $E(A)G$ in subseries EAAB, EAAC. [Derived from (EA line of) Type $E(A)G$.] Understanding of the operculum in the species of EF, EAAB, EAAC has come only recently, independently through the investigations of Carr and Carr, Johnson, and Pryor and Knox.

Type $IS(B)$: *Calyx* of free deciduous sepals pushed off at an early stage by enlargement of the opercular *corolla* : *Idiogenes*, *Symphyomyrtus* sections SB *Equatoria* and SS *Howittaria* (which as discussed below should probably be included in SB), also (probably by secondary phylogenetic reduction and loss of ring-meristem stage of calyx) in some species of section SI *Bisectaria* and again in section SW *Sebaria*. [Derived in I and SB–SS from Type A as in early ancestral forms or possibly through a Type $E(A)G$ stage as in *Gaubaea* ; probably derived from Type $SBC(C)$ in SI.   In SW it is less likely that the calyx was ever truly opercular.]

Type $SBC(C)$: *Calyx* opercular, shed before anthesis (sometimes very early), leaving a scar detectable by a break in the cuticle at the rim of the hypanthium in older buds ; *corolla* opercular : *Blakella*, *Corymbia* section CC *Ochraria*, most of *Symphyomyrtus* [sections SD *Tingleria*, SE *Transversaria*, most of SI *Bisectaria*, SL *Dumaria*, SN *Exsertaria* (which must include the so-called section SQ *Umbrawarria* of PJ_1), SP *Maidenaria*, most of SU *Adnataria*]. [Derived separately (i) in B and CC from Type $C(A)S(U)$ by ontogenetically earlier cessation of growth and abscission of the calycine operculum, (ii) in S from an early ancestral Type A condition, but probably not from the $C(A)S(U)$ or $IS(B)$ Types as at present represented.]

Type $C(A)S(U)$: *Calyx* opercular and shedding at anthesis with the opercular *corolla*, to which it is more or less intimately appressed [but, unlike $E(F)$, without primordial fusion between the whorls] to form an apparently single operculum, thus no calyx scar is present before anthesis : *Corymbia* section CA *Rufaria*, *Symphyomyrtus* section SU *Adnataria* in part (series SUJ, SUL, SUN, SUX). [Derived separately, (i) in CA probably direct from an angophoroid Type A ancestor, (ii) in SU *on several distinct occasions* from Type $SBC(C)$ by continued growth of the calycine ring-meristem and delayed abscission (in some species such as SUNAA *E. argophloia* and SUNCC *E. porosa* the calycine operculum may abscind just before the corolline).]

Type M : *Calyx* opercular, with usually only two tip primordia ; *corolla* completely lacking even as primordia : *Monocalyptus*. [Derived probably separately from other lines at an early epoch, though doubtless through unknown stages from an early Type A ancestor ; we can only guess at the stage at which

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* *Derivation* will usually denote phylogenetic change in what follows, while *development* will refer to ontogeny or organogeny, unless the context clearly indicates otherwise.

the corolla was lost—perhaps it was before operculization of the calyx.] The operculum of *Monocalyptus* (≡ section MA *Renantheria*) has been misinterpreted in the past but its nature has recently been established by Pryor and Knox (1971); it is very strong evidence against the hypothesis of Carr and Carr (which a decade ago I also tended in part to favour) of a close affinity between *Eudesmia*, *Gaubaea*, *Idiogenes*, and *Monocalyptus* (of PJ_1), and their consequent grouping as " *Eucalyptus* " *sensu* Carr et Carr.

(2) *Inflorescence.* (a) *Unit Inflorescence.* The basic inflorescence in the Myrtaceae appears to be thyrsoid, with dichasial branching as one would expect
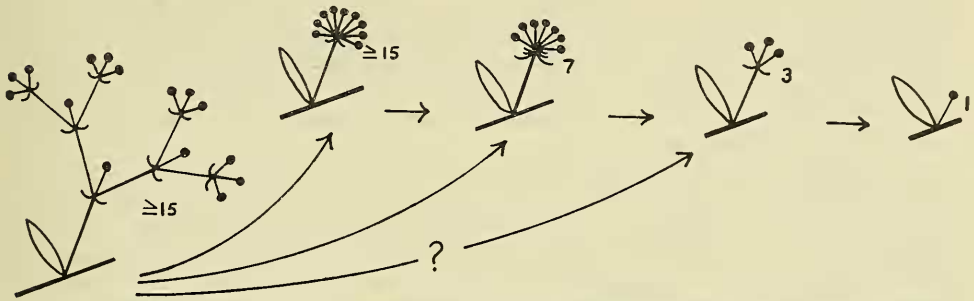
Fig. 2. Derivation of eucalypt umbellasters (unit inflorescences) from an indefinite dichasium. For further explanation see text.
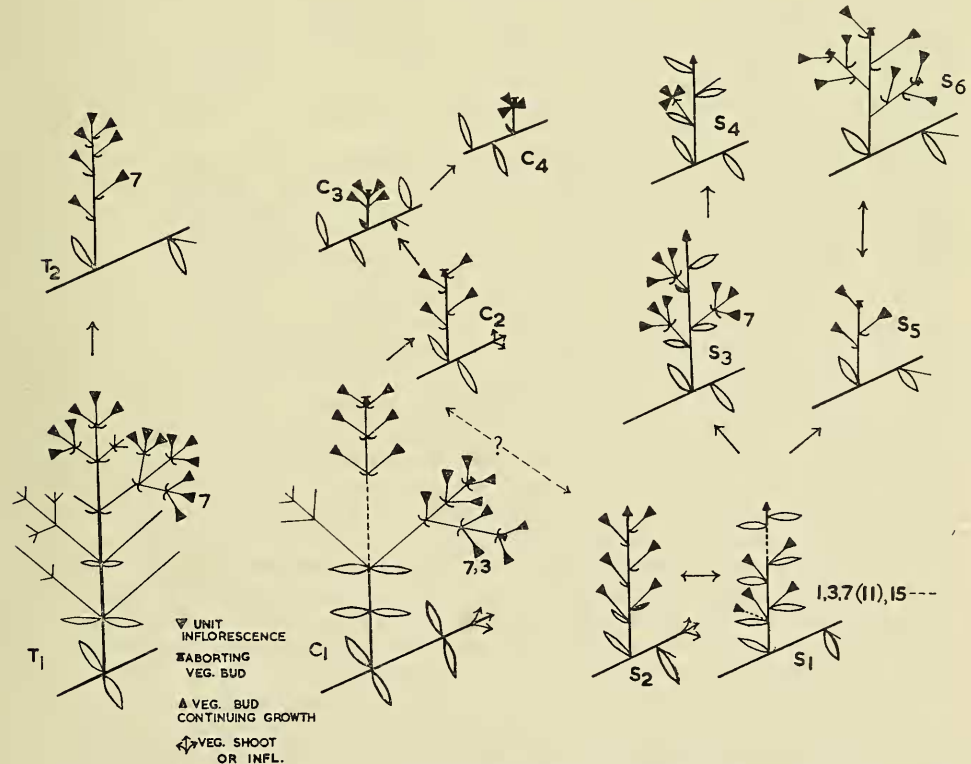
Fig. 3. Conflorescence types of eucalypts, and their suggested derivations. For further explanation see text.

in a family with primarily opposite and decussate phyllotaxy. If we were to take type T_1 of Fig. 3, but suppose the branches to end in individual flowers instead of unit inflorescences, it would correspond in general pattern with such a dichasial thyrse. More or less unreduced inflorescences of this type may be found in many Myrtoideae and in some Leptospermoideae (particularly Metrosiderinae *sens. lat.*), and by a comparative approach one can see how even the highly reduced inflorescences of such genera as *Callistemon* and *Leptospermum*, in their several ways, are derived from dichasial thyrses.

Eucalypt inflorescences are usually described as consisting of " umbels ", but (see Pryor and Johnson, 1971, pp. 2–4 and refs. therein) the basic unit inflorescence is clearly a condensed dichasium, which is itself of course derivable from a thyrse simply by termination of each axis in a flower after the *first* node. The number of flowers (f) in a dichasium is given by $f = 2^n - 1$, where n is the order of branching attained. Figure 2 illustrates diagrammatically the derivation of the umbelliform cymelets (" unit inflorescences ") from a dichasium (each plane of branching is actually orthogonal to the previous, but the whole is shown in two dimensions in the figure).

I shall coin the term *umbellaster** for such a unit (Latin *umbella*+-*aster*, suffix connoting " sham ", as in " poetaster ", etc.). Umbellasters may contain the full dichasial branching of the various orders, thus differing from a normal dichasium only in the non-elongation of all internodes except the first (peduncle) and the last (pedicel) and sometimes in the partial or complete suppression of bracts of higher orders (the first pair is always present, though deciduous and sometimes fused into a calyptra). Thus for $n = 1, 2, 3, 4, 5$ we should have umbellasters with 1, 3, 7, 15, 31 flowers. However, as Carr and Carr (1959) have pointed out, due to crowding and suppression in the umbellaster bud, branching may be monochasial at higher orders, and a familiar case is the 11-flowered umbellaster in which only one flower of each pair is produced at the final branching. Even where the flower number of 15 is found it may be due to two stages of monochasial branching from a dichasium of 7, rather than representing a fourth-order dichasium.

Possibly the umbellaster condition was separately derived more than once from uncondensed dichasia, and indeed umbelliform inflorescences occur occasionally in other Myrtaceae, e.g. some species of *Backhousia*. The most common flower number is 7, with 3 also frequent ; phylogenetic reduction in number, sometimes associated with increase in flower- and fruit-size, seems to have been common, but increase to numbers above 15 is also quite likely. Carr and Carr (*l.c.*) object to Pryor's earlier reference to the single axillary flower of some species as " the ultimate stage of reduction from an indefinite dichasial cyme . . . " because of their emphasis on ontogeny, and say that " even from the point of view of phylogeny, Pryor's statement would be misleading ". Pryor's statement *was* made from the point of view of phylogeny (informed by ontogeny), as is my present comment, and if one looks widely at the Myrtaceae it is evident that it is not misleading. The cited paper reports very valuable developmental studies but, in its account (and inferences therefrom) of an aberrant individual of SNEEP *E. camaldulensis* as if it represented a characteristic condition for the species, as well as in its suggestion that the three-flowered umbellaster is primitive even for such groups as *Corymbia*, it shows how ontogeny without a broad comparative and phylogenetically oriented background can be misleading indeed.

There are tendencies to certain flower numbers in some of the sections, and more particularly in some series and subseries, but in general the number in the

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* This term is explicitly intended to include conditions in which the flowers are sessile. Carr and Carr (1959), like some others whom they cite, extend the term *umbel* to cover the fundamentally different, sympodial umbellaster, but nevertheless exclude the trivial variants in which the pedicels do not elongate.
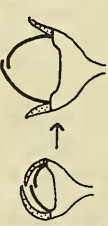
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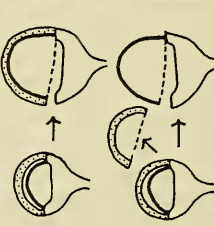
umbellaster seems to be a fairly flexible character evolutionarily, though it is often constant at the species or subspecies level, and especially so in individuals [contrary to the report of variation in SPIAC *E. kitsoniana* by Carr and Carr, *l.c.*, which our evidence does not confirm as the usual condition even in that species]. Various developments of bracts are found, and also the interpolation of an intranod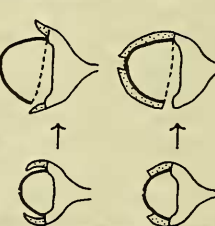e to produce a " stepped " $4+3$ umbellaster (as in some species of SU *Adnataria*). Carr and Carr (*l.c.*) may be consulted for descriptions of these, but with caution as to the interpretations. In certain species the apparent " umbels " described by earlier authors are in fact compounds of several umbellasters (see below).

(b) *Conflorescence.* As a purist (or pedant ?), I use *conflorescence* in preference to the Graeco-Latin mongrel " synflorescence " (as used by Troll, 1964, and others) to cover shoots or shoot-systems bearing a number of " unit inflorescences ". In many plants one cannot define unit inflorescence and conflorescence in any clearly exclusive way, but this is not a difficulty in *Eucalyptus* if one examines the structures concerned carefully and comparatively.

Figure 3 illustrates broadly the patterns and probable or possible phylogenetic trends in eucalypt conflorescences. The unit inflorescence shown in these diagrams is an umbellaster, and the numerals placed near some of these indicate the most usual flower number in the types concerned. The column " Inflor." in Figs 4 and 5 gives the conflorescence types characteristic of the subgenera (sections are also indicated in *Symphyomyrtus*).

I shall discuss the main trends briefly ; it is to be understood that some of the phylogenetic derivations probably occurred more than once. The diagrams are generalized, and further variations, which may be adaptively important, are found in the number of internodes and development of intranodes (between the two opposed members of a leaf- or bract-pair, leading to a quasi-alternate but still decussate phyllotaxy). Variations occur also in the position of the umbellasters or sometimes conflorescences on a year's shoot growth (*basitonic, mesotonic, acrotonic* from proximal to distal) as discussed by Carr and Carr (1959). These are partly correlated with the various conditions illustrated but, unless leading to a conflorescence of obviously different appearance, are not separately shown in Fig. 3. Duration of bud development also varies, sometimes extending over two years with a marked diapause ; clearly, this is also of adaptive significance in relation to climate.

Type T (" terminal ") conflorescences may well represent a very early separate line from the remainder. In these the main and all other axes terminate in an umbellaster and thus in a flower ; hence the conflorescence is truly a terminal type. The expanded subtype T_1 characterizes the small tropical sections SB *Equatoria* (including the well-known SBA:A *E. deglupta* of eastern Malesia) and SS *Howittaria* (which in PJ_2 may well be included in *Equatoria*). In PJ_1 we have referred these to *Symphyomyrtus* but perhaps they represent a separate phylad as indicated in Fig. 1. The reduced subtype T_2 is found in *Idiogenes* which consists of that notorious bone of contention IAA:A *E. cloëziana*. So far as I have checked, truly terminal conflorescences occur in no other section, although in some species of *Eudesmia* conflorescences of subtypes S_3 and S_4 (see below) may possibly be primitively and not secondarily terminal as I have tentatively suggested. Subtype S_3 structurally resembles a shoot bearing a series of reduced T_2's but, on the general resemblance of species bearing this subtype, I would regard S_3 as a secondary development of S_1. *Idiogenes* ($\equiv$ section IA *Gympiaria*) differs in ovule and seed type from *Symphyomyrtus* whereas *Equatoria* and *Howittaria* do not appear to do so ; thus their mutual affinity is not to be too readily assumed. As mentioned earlier, however, there is a correspondence in operculum type between the three groups with type T conflorescences.

SUBGENUS	FLOWER BUD: YOUNG, ANTHESIS	ANTHER	COTYLEDONS	INFLOR.	OVULE	HAIRS	BRISTLE GLANDS	PITH DUCTS, GLANDS	PSYLLID
[GENERALIZED ANCESTOR]			?	DICHASIAL THYRSE		a?			
ANGOPHORA				c_1	h	a(≥2)	+	D, G	
BLAKELLA				c_2, c_3, c_4	h	r(B),—	+	±D, G	
CORYMBIA				c_1 c_2	h	a(1),—	+	D, G	
EUDESMIA				s_1, s_3, s_4	h	r(E)	—	—, G	G, —

SUBGENUS	FLOWER BUD: YOUNG, ANTHESIS	ANTHER	COTYLEDONS	INFLOR.	OVULE	HAIRS	BRISTLE GLANDS	PITH DUCTS, GLANDS	PSYLLID
GAUBAEA				C_1, C_3	a	—	—	—	—
IDIOGENES				T_2	a	—	—	—	—
MONOCALYPTUS				S_1	a	$r(M), -$	—	—	S
SYMPHYOMYRTUS				T_1 (SB, SS) S_1 (SE, SI, SL, SN, SP, SU) S_2 (SD) S_3 (SNI) S_5 (SU, SW) S_6 (SU)	h	—	—	$-, \pm G$	G, —

Figs 4 and 5. Occurrence of certain features in eucalypt subgenera and sections. "Inflor." column gives conflorescence types as in Fig. 3. "Psyllid" column refers to *Glycaspis* subgenera only (G = subg. *Glycaspis*, S = subg. *Synglycaspis*): other genera of Psyllidae are also found on eucalypts. For further explanation see text.

Type C (" corymbioid ") conflorescences are characteristic of the *Angophora-Blakella-Corymbia* trio, though also found in the quite different *Gaubaea*. Superficially resembling type T, the C_1 subtype especially is often described as terminal and such conflorescences often do in fact mark the end of growth of their shoots. However, all of type C differ fundamentally from type T in that the main and branch axes do not end in umbellasters but in small, aborting, vegetative buds or tips. In the more reduced (derived) subtypes C_2, C_3, C_4 the conflorescence is usually or always borne laterally on a leafy shoot, as seen in series CCC *Maculatae* (the " Spotted Gums "), and in the more reduced *Blakella*. In the latter case the bracts subtending the umbellasters may be lacking, and in some species (e.g. BAA:D *E. grandifolia*) the umbellasters are sessile in a cluster which is itself umbelliform but includes a tiny abortive vegetative tip. Such cluster-like conflorescences were confused with umbellasters (themselves not then understood) and described as " umbels " by Blakely and earlier authors. Blake (1953), who first apprehended the coherence and limits of this group (his *Clavigerae*, a name also used for the single series BAA in PJ_1), appreciated the compound nature but did not make clear the equivalence with the *Corymbia* conflorescence.

Type S (" simple ", despite some secondary derivatives !) conflorescences are the most common (Figs 4, 5) and are characteristic of *Eudesmia*, *Monocalyptus*, and *Symphyomyrtus* (excepting SB and SS). Some of the variants are virtually identical in pattern with variants of type C, with which they share the fundamentally " non-terminal " condition. However, type S (except in a few probably derived cases such as EAADE *E. gamophylla* in *Eudesmia*, and many of section SU *Adnataria* in *Symphyomyrtus*) is distinguished by continued growth of the vegetative tip either during or after flower-bud development, and by the evidently basic condition of simple umbellasters borne in the axils of foliage leaves.

This basic S_1 pattern may well have arisen more than once, probably by reduction from ancestors with simple lateral dichasia in the leaf axils. It is universal in the very well-defined *Monocalyptus*, where it has undergone little secondary change (though the umbellasters themselves range from 3- to >30-flowered) ; it is the most usual condition in *Eudesmia* (umbellasters most commonly 3-flowered but in some species 7- or many-flowered) : it is very widespread in *Symphyomyrtus* (umbellasters very often with 7, quite often with 3 or 11, less frequently with 1 or $\geqslant$15 flowers). Superposed twin umbellasters may be found in some axils, for instance not uncommonly in section SI *Bisectaria* ; these do not show any common rhachis or secondary bracts (so far as I know) and are probably a phylogenetically secondary development associated with the presence of supernumerary axillary buds.

The S_2 condition of the curious " Yellow Tingle ", SDA:A *E. guilfoylei* (the sole species of section SD *Tingleria*) is fairly clearly due simply to reduction of subtending leaves to a bract-like state. Its continuing growth shows it to be basically distinct from the superficially similar " racemes of umbels " of, say, IAA:A *E. cloëziana* (type T_2) and to a lesser degree from the conflorescence of SWA:A *E. microcorys* (type S_5, elongated). *Eudesmia*, as mentioned, shows some odd conditions and the apparent " umbels " in, for example, EAACM *E. jucunda* or EAADA *E. gongylocarpa* are probably clusters of umbellasters of type S_4—but they need further investigation.

In *Symphyomyrtus*, subtype S_3 occurs only once, in SNI:A *E. michaeliana*. This rather perplexing species seems to be closest in leaf-venation, seeds, etc., to the " Red Gums " of section SN *Exsertaria* and its peculiar axillary triads of umbellasters are here tentatively interpreted as a secondary expansion of the S_1 condition by an interpolated dichasial branching. A study of inflorescences in hybrids, if they can be made, may help to elucidate this. *E. michaeliana* needs more study morphologically, chemically, and by breeding experiments to determine whether our hypothesis as to its position is justified. It does not

seem to have much in common with SB *Equatoria* and SS *Howittaria* to support any suggestion that its three-umbellaster groups are reduced T-type conflorescences.

In section SU *Adnataria*, the " true Boxes and Ironbarks ", sub-type S_1 is found as well as conditions transitional to, and fully characteristic of, sub-types S_5 and S_6. These are the " terminal, paniculate inflorescences " of the older describers of the species concerned. The condition like T_1 and C_1, yields a massing of flowers towards the ends of the branches and doubtless has adaptive significance. Its derivation from S_1 is clear, as is that of section SU from the basic stock of *Symphyomyrtus*. The " Tallow-wood ", SWA : A *E. microcorys* (constituting section SW *Sebaria*) has a similar inflorescence but is an isolated species whose links with the rest of *Symphyomyrtus* are still obscure.

The remaining features to be mentioned require, or allow, only a briefer treatment. References are given only when they are not covered in Pryor and Johnson (1971) or otherwise need special mention.

(3) *Androecium*. (a) *Anthers*. Figures 4 and 5 summarize the anther types, which are more fully illustrated by Blakely (1934, 1965). The attachment of the filament to the connective is not shown, but the primitive dorsal attachment and versatile condition is indicated by the letter " v ", and is retained in all groups except some sections of *Symphyomyrtus*. Here more basal attachment and the semi-versatile condition are associated with the series SIX *Calycogonae* (left anther of " sv " pair in Fig. 5) and SIZ *Foecundae* (right anther of " sv " pair) of section SI *Bisectaria*, while completely adnate anthers with more or less pore-like openings are characteristic of section SU *Adnataria*. The usual (" porantheroid ") condition in the latter is as in the left-hand of the " a " pair, but in the three series SUT *Polyanthemae*, SUV *Paniculatae*, and SUX *Melliodorae* the so-called " terminales-type " anther (right-hand of the " a " pair) is found. No breeding barrier exists between species with these two anther types, and the division on anthers cuts across that on persistence of calycine operculum [see above under operculum-type $C(A)S(U)$]. Hence until more information is available on other characters we cannot say whether the anther or the operculum condition (or both) arose more than once.

The generalized " macrantherous ", versatile anthers with long, separate dehiscence-slits are variously shortened in some series but these variants are not separately shown. Small anthers with short, somewhat divergent loculi (top left of *Symphyomyrtus* group) are found in SB and SS, the *Equatoria-Howittaria* group, which may need to be excluded from *Symphyomyrtus*. A unique, specialized anther type (bottom " v " of *Symphyomyrtus* group) characterizes the single species of SD *Tingleria*. The " renantherous " type with the loculi confluent at the top was once thought to be a defining character for the " *Renantherae* ". From these the sections SB and SW have now been removed, and it has been shown that the bulk of the " *Renantherae* " belong together with a few species (series MAA *Preissianae*) which exhibit the primitive " macrantherous " anther type, and also with some intermediates (series MAB *Diversifoliae*) in *Monocalyptus* (in which PJ_1 recognizes only a single large section MA *Renantheria*). Thus the renantherous anther type is of later origin than the separation of the *Monocalyptus* line.

(b) *Other androecial features*. Other features of the androecium are also useful in classification and of evolutionary interest but can only be mentioned. They include (i) the so-called *staminophore* (*androphore* would be a happier term) or staminal ring, (ii) the grouping of stamens into four clusters evident in many *Eudesmia* species and occasionally elsewhere, e.g. in SW *Sebaria*, (iii) the development or otherwise of oil-glands in the filaments [a nice series is shown, for instance, from MAA *Preissianae* (abundant, large glands) through MAB

Diversifoliae (few, small glands) to other series of *Monocalyptus* (without glands)],
(iv) the more or less staminodial condition of the outer stamens in certain groups,
e.g. EAAD *Odontocarpinae*, SIX *Calycogonae*, SUJ *Ochrophloiae*, SUV *Paniculatae*,
and SUX *Melliodorae*, a feature which has clearly had multiple origins, (v) various
conditions in the flexure of filaments, which are inflexed in young buds even if
straight in mature buds with long opercula such as those of SICB *Cornutinae*,
and in the apposition of anthers to the disc* (e.g. in SL *Dumaria*).

The detailed study of pollen by electron microscopy may yield information
of classificatory and possibly phylogenetic value.   Pollen-morphological examina-
tion with the light microscope has not been very helpful in *Eucalyptus*.

(4) *Gynoecium and Associated Features.*   (a) *Ovary, style, etc.*   No discussion
of these features is yet possible which would be of much taxonomic or phylo-
genetic significance, except as treated under (b).   We may look hopefully to
others currently studying the development and morphology to bring forth some
illuminating discoveries in this field.

(b) *Ovule and seed.*   Arrangement of ovules and ovulodes on the placenta
has been studied by Carr and Carr (1962, 1963) and may prove to have consider-
able value in elucidating phylogenetic relations within *Eucalyptus*, and also
between particular groups of *Eucalyptus* and other genera, as mentioned below
under the discussion of possible polyphylesis. I have not yet examined placenta-
tion and ovule arrangement extensively and cannot comment upon them in
detail.

Two basic ovule types, the *anatropous* and the *hemitropous*, are found in the
eucalypts (Gauba and Pryor, refs. in Pryor and Johnson, 1971) and are associated
with certain seed characters, especially the presence of a raphe in the anatropous
type, as one would expect.   These and other seed characters, notably the varying
degree of development of the inner epidermis of the outer integument as a crystal
epithelium, cannot be elaborated here.   They strongly support the PJ_1 scheme,
especially in the complete separation of *Gaubaea* from *Eudesmia*, the inclusion
of EFC *Miniatae* in *Eudesmia*, the affinity of *Angophora*, *Blakella*, and *Corymbia*,
and the marked difference between those three and both *Eudesmia* and *Gaubaea*.
Sectional groupings within *Symphyomyrtus* are also supported by seed characters
but these need more study.   Ovule and seed types appear to associate *Idiogenes*
with *Gaubaea* rather than with SB *Equatoria* and SS *Howittaria*, although *Idiogenes*
resembles these latter in its T-type conflorescence and Type *IS(B)* operculum.
Further comparisons may tell us in which of these characters convergence must
be invoked.

Figures 4 and 5 show only the anatropous-hemitropous distinction ;   the
anatropous is most general in Myrtaceae but campylotropous or hemitropous
ovules do occur elsewhere in the family, for instance in *Arillastrum* (Dawson,
1970, and see below).   Most interestingly, the seeds of GAA : A *E. curtisii* are
extremely similar externally and anatomically to those of *Tristania conferta*.
Tristania as currently recognized is a heterogeneous group and should probably
be split into three genera.   Clearly, the resemblances and differences between
Gaubaea (and other subgenera) and the components of *Tristania* and their allies
will need much deeper investigation.   It is of course not necessarily the case
that either all the hemitropous or all the anatropous subgenera belong together
phylogenetically.

(c) *Fruit (including fruiting hypanthium).*   Features of the fruits are of
course used a great deal in distinguishing and circumscribing the species and
subspecies of *Eucalyptus*, and many of these features run through series, sections,
or even subgenera.   It is easy, for instance, to recognize an *Angophora*, a *Blakella*,

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* Carr and Carr prefer to term this the nectary ; it is nevertheless a floral disc in the general
sense in which that term is employed in taxonomic description.

or a *Corymbia* by its fruit and, on a lower level, the fruits of *Monocalyptus* series MAH *Capitellatae* (the "true Stringybarks") are all patently variations on a theme, as are those of *Symphyomyrtus* series SIC *Cornutae* or SIT *Oleosae*. It has not as yet been so easy to describe or define the whole congeries of characters which hold the major groups together, or to discern trends which may be phylogenetically interpreted.

(5) *Cotyledons*. These will not be discussed in detail. Some idea of the types characteristic of the subgenera is given in Figures 4 and 5. The angophoroid group A, B, C clearly hangs together and so do the sections of *Symphyomyrtus* with their emarginate (bilobed) cotyledons (though the dubiously included SB and SS need to be checked). The right-hand figure for *Symphyomyrtus* shows the "bisected", Y-shaped cotyledons characteristic of the large section SI *Bisectaria* for which other positively uniting characters are still being sought, though the process of taxonomic agglomerative clustering (on a non-numerical basis at present) tends to associate the various series of this section. Y-shaped cotyledons occur also in SLUBA *E. dundasii*, which on other features appears to belong to section SL *Dumaria*, a group which seems to have radiated in parallel with *Bisectaria* but has retained the broader, bilobed cotyledons of the rest of *Symphyomyrtus*. The description by Carr and Carr of certain small outgrowths as cotyledonary stipules is open to further study and interpretation. Stipules are not a general feature of Myrtaceae.

(6) *Emergences*. (*a*) *Trichomes* ("*hairs*"). Hairs are found on various organs, most often juvenile shoots and leaves but also sometimes on adult shoots and even inflorescences and hypanthia. They need detailed anatomical study and their significance cannot be fully assessed.

Type "a" (Figs 4, 5) comprises "angophoroid" hairs arising singly from undifferentiated parts of the epidermis. They are either uniseriately several-celled as in *Angophora*, or single-celled and very short as in *Corymbia*. I have not found hairs of this type in *Blakella*.

Type "r" comprises radiating uniseriate hairs which arise in clusters from more or less raised oil glands. Three sub-types are recognizable at sight but not yet accurately described or analysed : I suspect that they have arisen independently in the course of phylogeny. They are found as follows : (i) subtype "r(B)" (blunt-ended, 1- or 2-celled, rather thin-walled hairs, often almost erect, on prominent glands or bristle-glands) in some species of *Blakella*, e.g. BAA : H *E. gilbertensis*. (ii) Subtype "r(E)" (blunt-ended, of rather thin-walled cells, on slightly prominent or flat glands) on juvenile shoots of all species of *Eudesmia*. (iii) Subtype "r(M)" (acute-ended, of rather thick-walled cells, on prominent glands) on juvenile shoots of all species of series MAH *Capitellatae* (these are the so-called "stellate hairs" of the Stringybarks) and of an undescribed species from south-eastern New South Wales (discovered after publication of PJ_1) which may require the establishment of a new series or subseries in *Monocalyptus*. Somewhat papilliferous raised glands are found on a few species (e.g. MAKCA *E. regnans*) of series MAK *Obliquae*, and these may be regarded as morphologically transitional between the "r(M)" condition and the hairless state of most of *Monocalyptus*. Hairs are reported from a few species of *Symphyomyrtus* ; the report by Maiden for SUABB *E. leptophleba* is false and evidently due to mixture of material, that for SICBE *E. lehmannii* is based on blunt several-celled papillae on the surfaces of glands. Significantly, hairs are absent in *Gaubaea* and *Idiogenes*, which were referred to *Eudesmia* (as "*Eudesmieae*") by Carr and Carr as recently as 1970 (see Pryor and Johnson, 1971 for discussion). Trichomes closely resembling the various eucalypt types do not seem to occur in other genera of the Myrtaceae, but simple hairs of rather different types are quite common in many genera.

(b) *Bristle-glands.* These (Figs 4, 5) are characteristic of the angophoroid trio *Angophora*, *Blakella*, and *Corymbia*, and are essentially elongated protruding oil glands, with a multicellular wall. In *Blakella* they are very thin and may superficially resemble simple trichomes, which has led to misdescription of species of this group. Some degree of elongation of raised oil glands occurs in other species and in young seedlings of MAKAA *E. obliqua*, for instance, these are quite bristle-like, though doubtless representing a parallel or convergent development. *E. obliqua* is quite unlike the angophoroids in other respects.

(7) *Oil Ducts and Glands in the Pith.* These are described by Carr and Carr (refs. in Pryor and Johnson, 1971) and are distributed as shown in Figs 4 and 5 (information partly from Carr and Carr, partly new observation). Once again the angophoroid A, B, C are linked, by the possession of oil ducts in the pith. Presence or absence of glands may be a fairly regular feature in some sections or series (e.g. most of the first half of the series of SI in the PJ_1 arrangement have pith glands, whereas SIP–SIZ inclusive lack them ; most of SL have pith glands ; SE, SN and SP lack them) but in other cases there is considerable variation even within series (as in those of SU). They are absent altogether from *Gaubaea*, *Idiogenes*, *Monocalyptus*, and SB *Equatoria* and SS *Howittaria*. In SP *Maidenaria* oil glands are reported in the secondary bark of older trees of most species but not quite all ; this feature appears to be peculiar to the section.

It is difficult to interpret these conditions in terms of trends (or adaptations) but they do aid in a polythetic classification. It should be remembered that oil glands are almost always present in the primary cortex and in leaves and some floral parts.

(8) *Chemical Features.* (References will be found in Pryor and Johnson, 1971, and in works cited therein).

(a) *Terpenes and other essential oil constituents.* This is a classical field in eucalypt chemotaxonomy, and indeed the work of R. T. Baker and H. G. Smith and their successors is classical in chemotaxonomy generally. The patterns tend to support PJ_1 but caution is necessary in interpretation, due to the possibility of switches in metabolic pathways which may be determined by quite simple genetic changes, and not necessarily very rigidly stabilized by selection so far as the oil constituent end-products are concerned. Information is hoped for soon on such critical groups as *Gaubaea*, *Idiogenes*, SB *Equatoria* and SS *Howittaria*.

(b) *Polyphenols.* The information in this field, due chiefly to the work of Hillis, has been presented according to Blakely's classification, and in a few critical cases is based on material of doubtful identification. I hope chemists will review it in relation to PJ_1 to see what light is shed thereby, and that they may be able also to interpret the significance of occurrences more clearly in the light of increased knowledge of biochemical pathways. At present I can only say that PJ_1 appears to be supported in general, especially in relation to the delimitation of *Monocalyptus* which contains (though not invariably) the distinctive substance renantherin.

(c) *Leaf waxes (chemistry and shape of cuticular deposits).* As pointed out by Pryor and Johnson (1971) this has proved a disappointing field, despite the thorough studies by Hallam and Chambers. Although there is a general fit to the broad classification of PJ_1, there is evidence of much parallelism, and the shapes revealed in the electron-micrographs seem often to be associated simply with glaucous *versus* non-glaucous conditions as seen with the naked eye, different types being found in obviously closely related species which are often within a single superspecies.

(d) *As reflected by host-insect associations.* This field has not been at all thoroughly surveyed but the large, lerp-forming genus *Glycaspis* (Hemiptera : Psyllidae) has been intensively studied taxonomically by Moore, and its associations are interesting at the subgenus level. No *Glycaspis* at all is known from *Angophora*,* *Blakella* or *Corymbia*, although one subgenus, *Boreioglycaspis*, is found on *Melaleuca*, which is only rather remotely related to any eucalypt. *Gaubaea* and *Idiogenes* are insufficiently examined but no *Glycaspis* is recorded from those subgenera either. The type subgenus *Glycaspis* occurs widely on *Symphyomyrtus* (no information from SB–SS, SD, and no record from SW although this has been searched) and on a few species of *Eudesmia* (both EA and EF) as well as, oddly enough, on *Tristania conferta* (which does *not* seem to be related to these eucalypt groups—see above). On the other hand the numerous species of subgenus *Synglycaspis* are confined to *Monocalyptus*. At sectional and lower levels in the eucalypts the occurrences of *Glycaspis* species seem to me to have much less taxonomic significance, and I would certainly not agree with Moore's suggestions that eucalypt-*Glycaspis* associations throw doubt on eucalypt relationships which are firmly established on other grounds. One can hardly do this when one finds the same *Glycaspis* species on species of SI and SU (e.g. *G. repentina*) or even of EA and SN (on both of which *G. onychis* occurs).

One could go on to discuss other features, e.g. wood and bark anatomy, leaf venation patterns, fungal pathogen susceptibility (such as the association of *Phytophthora cinnamomi* and *Monocalyptus*, or *Ramularia* and the angophoroids), epidermal anatomy (a possibly promising field in which work has begun by scanning electron microscope techniques by the Carr group and others). But this would not add much to the picture at this stage. Neither would the scanty fossil evidence, which provides no detailed background of the phylogenetic history. Chromosome numbers are depressingly constant (see Pryor and Johnson, 1971).

DISTRIBUTION OF GROUPS AND CHANGES IN THE CLASSIFICATION

Distributions of the subgenera and sections are of interest and are shown in a general way in Table 1. It would perhaps be better to use phytogeographic divisions rather than States, but to do so would have involved difficulties of compilation.

Table 1 is compiled to recognize some small changes from PJ_1; we know a little more about some distributions, and with further study have altered our views on a few species and subspecies. Apart from the species mentioned above under " Trichomes ", the most interesting specific case concerns *E. pachycalyx*, referred with doubt in PJ_1 to the synonymy of SNABAA *E. alba* [ssp. *alba*], in the absence of the Type specimen (apparently lost while on loan some twenty years ago) or any other material. *E. pachycalyx* has now been rediscovered and, having examined twigs, leaves, buds, flowers, fruits, seeds and cotyledons, I am convinced that it belongs in section SI *Bisectaria*. I here assign it the code SIQ:E, placing it in series SIQ *Squamosae*, although it differs in bark type and other details from SIQ:A *E. squamosa*, the other strictly eastern member of *Bisectaria* [SIR:E *E. bakeri* is merely the eastern vicariant of the central and western SIR:A *E. jutsonii* s. lat.]. It is most remarkable to find a true *Bisectaria* in north-eastern Queensland, adding to the mystery of why this species and *E. squamosa* should have reached the humid east. In other series of *Bisectaria* only eremaean species appear to have crossed the continent. Likewise, why did *Bisectaria* radiate and flourish so exceedingly in the west while its *Squamosae* representatives (which are hardly primitive in the section) barely hang on in the east ?

Another change from PJ_1 is the elimination of section SQ *Umbrawarria*. I am now convinced that its sole species, *E. umbrawarrensis*, is closely related to

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* Except one very doubtful record of subgenus *Glycaspis* on BAA:A *E. tessellaris*.

SNABG *E. brevifolia*, and assign it the new coding SNABI. Further, " SLI:G *E. comitae-vallis* " is in fact, so far as the Type specimen is concerned, a probable hybrid : SLI:I *E. concinna* × SLUAA *E. ovularis* (syn. *E. cylindrocarpa*, not the undescribed SLUAC to which the name " *E. ovularis* " has been misapplied in Western Australia). *E. brachycorys* is not, then, a subspecies of " SLI:G " but appears to be a member of series SLU *Dundasianae* subseries SLUA *Ovularinae*, and I here assign it to the coding SLUAK (Mr. M. I. H. Brooker, pers. comm., suggested this affinity for *E. brachycorys*, and I agree with it).

A question for the future will be to determine whether there are general adaptive tendencies in the several sections and subgenera which are linked to their present distributions and the climates and conditions of their geographic origins, if those can be determined.

ARE THE EUCALYPTS POLYPHYLETIC ?

Elevation of some or all of the subgenera to generic status would be obligatory, at least in my view, if we were to become convinced that their phyletic relationships lay more closely with other genera of the Myrtaceae than with each other. I suspect that this may in fact be so.

It is possible, as we have seen, that *Gaubaea* is related to *Tristania*, while *Angophora-Blakella-Corymbia* may well be more closely related to *Arillastrum* (*Spermolepis*), a very interesting New Caledonian genus studied by Dawson (1970). Dawson has shown that *Arillastrum* should not be placed in Metrosiderinae if that subtribe is reasonably restricted in its content and circumscription. Unlike the *Metrosideros* alliance, *Arillastrum* has stamens (some staminodial) in many whorls, ovulodes as well as normal ovules and these arranged in a definite pattern, campylotropous ovules (not very different from the " hemitropous " type of some eucalypts), a crystal layer in the seed-coat, and broad reflexed cotyledons. The petals are not as broad-based as in *Angophora* but are less clawed than in many Myrtaceae and have a median thickened area. I emphatically do not suggest that *Arillastrum* is to be regarded as representing any kind of ancestor of any group of eucalypts ; nevertheless it shares a number of characters with several of the " hemitropous " set of eucalypt subgenera, although it differs variously from all of them. Dawson has pointed out that *Tristania* (s. lat.), and *Xanthostemon* also, should be separated from the *Metrosideros* group, although they have retained the anatropous ovule condition. *Eucalyptopsis*, which resembles eucalypts in seeds, cotyledons, and of course in having an operculum, may also be related to some of the eucalypt lines.

Correlation of the results of Dawson's continuing work with that of students of " *Eucalyptus* " (I dare now to put it in quotes !) should be of the greatest interest to the phyletic taxonomist and to the phytogeographer. We must, I think, seek the origins of the eucalypt lines near the very roots of subfamily divergence in the Myrtaceae, although I would not support the suggestion of Pilipenko (1962) that " *Eucalyptus* " is derived from " *Eugenia* " (itself a heterogeneous assemblage) ! If the eucalypts are indeed polyphyletic in this broad (subtribal) sense, then they present an even more remarkable example of parallel and convergent evolution, presumably in response to environmental selection, than has been thought.

CONCLUSION

I have discussed with varying degrees of sketchiness some of the observed characters and the apparent trends in them, in relation to the PJ_1 classification. Naturally I consider that they support this classification, within the general limitations of classifications as discussed at the beginning of this address. If I did not, then I should change the classification, and have indeed suggested some possible changes for checking. The suggestion of polyphylesis from rather widely separate origins is, I suppose, the most radical and far-reaching, but it

calls for more substantial evidence before incorporation into the formal system. Uncertainty at this level does not vitiate the detailed system at lower levels.

Space is lacking here to recapitulate the various and complex hypotheses involved ; they are implicit in PJ$_1$, to some extent in Fig. 1, and in the foregoing discussion—and they can be dragged into the light by those who will, I hope, help to investigate them.

As a gratuity to those critics who regard speculation as a scientific sin, I refer them to the quotation from A. N. Whitehead which is the ironic text for this address. I am not very attracted by formalism and rigidity in science (though I am grateful that there are some who are) and would venture that even in the Queen of the Sciences mathematicians of insight and wide-ranging interest would agree that somewhat imprecise visualization of things as a whole, and gathering of many threads of thought and fact, can be as profitable as the equally necessary punctilious following-through of detail. In this small field of eucalyptology, such a two-pronged approach should also be productive. We have generated some hypotheses—it is for the next few years to show how good or bad they are.

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Note : For other authors mentioned in the text without dates the references (sometimes numerous) will be found in Pryor and Johnson, 1971.